

GEOGRAPHICAL ASPECTS OF BIRD-FLOWER COEVOLUTION, WITH PARTICULAR REFERENCE TO CENTRAL AMERICA¹

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ABSTRACT

The overall objective is to compare the ecological impact of bird-flower coevolution in different geographical areas. However, it is first necessary to define the parameters of such coevolution in broader terms than those of the traditional "syndrome of ornithophily," which focuses very narrowly on some aspects of floral morphology. I recognize three distinct components of flower function: attraction, reward, and filtering mechanisms, and discuss their functioning in an ecological context, and as they relate to the genetic system or "pollination unit" of the plant. Then I turn to nectar-feeding birds, and discuss not only morphological, but ecological and behavioral specializations to flowers as a food source. These discussions develop explicitly my criteria for detecting and evaluating bird-flower coevolution. The different groups of birds known to feed regularly (as opposed to opportunistically) on nectar are then compared according to these criteria, to determine their relative degrees of specialization for, and dependence upon, a high-nectar diet. Different groups are found to vary widely in their degrees of specialization for flower-feeding, and it is evident that bird-flower coevolution has followed very different courses, and led to widely divergent ecological systems in different geographical areas. By any criteria the hummingbirds are the most specialized avian nectarivores, although they are approached in this regard by some members of certain passerine groups, notably among the sunbirds. Several groups of passerine nectarivores also occur with the hummingbirds in many New World areas; these groups show low to moderate degrees of specialization for nectarivory, either as pollinators or as parasites on the hummingbird-flower system. The New World tropics thus present a wide range of specializations for flower-feeding in their avifauna, and represent a particularly interesting area for study. Patterns of ornithophily and nectarivory are thus examined in detail for this area, concentrating specifically on Southern Central America, especially Costa Rica. The altitudinal and geographical distributions of the two main groups of hummingbirds, the hermits and nonhermits, are found to differ, as are the taxonomic and ecological affinities of their primary foodplants. The hermits are most numerous in wet lowlands and the adjacent foothills, and are primarily associated with large monocotyledonous herbs, notably *Heliconia*. The nonhermits reach their greatest taxonomic and ecological diversity in the lower middle elevations, and are the only group present at high elevations; they seem to have coevolved with the flowers of a variety of dicot families, and the bromeliads among the monocots. Passerine nectarivores occur primarily as parasites on the hummingbird-flower system (Coerebidae) and are important as pollinators only in seasonally dry areas when the hummingbirds are poorly represented.

Within the last ten to fifteen years the study of pollination has passed from a purely botanical pursuit to an extremely active field of ecology. This is especially true with respect to bird pollination systems: a resurgence of interest in the foraging ecology, energetics, and social behavior of nectarivorous birds is leading to a new and broader appreciation of their role as pollinators. This, in turn, is one of the major catalysts in the continuing emergence of a more balanced and

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profound view of plant-pollinator coevolution. This new outlook is still evolving rapidly, and rather than attempt a theoretical synthesis, I will apply some of these new points of view to a geographical survey of bird-flower coevolution.

My specific objective is to compare the kinds and degrees of coadaptations between birds and flowers in different geographical areas, hoping thereby to arrive at a better understanding of the ecological and evolutionary impact of these coadaptations in different biota. By coadaptation, I am referring to the degree of ecological interdependence of bird and flower, as well as to the degree of morphological correspondence (as embodied by the well-known "syndrome of ornithophily"). The most highly coevolved system, then, is one in which the flower is completely dependent on the bird for pollination, and the bird requires the energy provided by the flower for breeding and molt: reproduction and perhaps even survival of either would be impossible without the other. Such coadaptation makes the species involved peculiarly vulnerable—what affects one will perforce affect the other—but it also makes possible the occupation of new ecological niches or adaptive zones (e.g., winter breeding in *Ribes speciosum* and *Calypte anna*, cf. Stiles, 1973).

In this paper I shall first review the kinds of coadaptations that can occur between birds and flowers, considering behavioral, physiological, and ecological as well as morphological parameters. I shall thereby develop criteria by which to compare the bird-flower coadaptations of different continents. I shall then discuss in more detail bird-flower coadaptations of the New World tropics, particularly Central America. Hopefully this analysis will lead to a deeper understanding of the ecological impact of these systems, and of the evolution of the groups of birds and flowers involved.

THE SYNDROME OF ORNITHOPHILY REVISITED

Until recently most studies of bird-flower coadaptations were devoted to demonstrating the existence of pollination by birds, and to elucidating the floral mechanisms involved. These adaptations are summarized in the well-known "syndrome of ornithophily" which represents the culmination of many years of observation and controversy (Faegri and van der Pijl, 1966), as well as a convenient starting point for the present discussion. Two things are immediately obvious from this "syndrome": the emphasis is narrowly focused upon the flower itself, ignoring many other aspects of the plant's biology that might affect bird visitation and pollination. Also, virtually nothing is said about possible specializations of birds for flower visitation.

In this paper I shall attempt to take a broader and less one-sided view of bird-flower coevolution. Elsewhere (Stiles, 1978b) I have discussed in some detail the various ways in which parameters of plant populations, and of the plant itself, can impinge upon pollination biology, with particular reference to bird pollination. For other discussions of this general theme, see Gadgil & Solbrig, 1972; Stiles, 1975; Wilbur, 1976; Pitelka, 1977; Bawa & Opler, 1977. Here I wish to emphasize aspects of floral biology *per se*, but without ignoring this broader context.

First, some definitions may be in order. Faegri & van der Pijl (1966) distinguish between "attraction unit" (those features that attract a pollinator from some distance away to the flower or inflorescence), and the "pollination unit" (within

which pollination occurs). In reality two distinct phenomena are being confused by these authors' use of "attraction unit": the attraction of the pollinators' *attention* to the flower, and the provision of a real or simulated reward that actually induces the animal to visit the flower. I restrict the term "attraction unit" (or component) to those mechanisms subserving the former function, and use "reward unit" (or component) for those accomplishing the latter. Clearly the functioning of the attraction component must be intimately related to the sensory biology of the flower visitors, while the reward component must correspond to some nutritional, sexual, or other need of the pollinator. Although this distinction may be blurred in some flowers (see e.g., Simpson, this symposium), it is clear enough in bird flowers: bright colors form the basis of the attraction component; nectar, of the reward component. Another function that I choose to distinguish is the restriction of access to the reward to a narrow segment of the potential spectrum of visitors attracted. The term "exclusion mechanisms" has been used here, but I prefer the term "filtering component" (or mechanism). At least in bird flowers, such limitations of the visitor spectrum are often not absolute exclusions but relative ones, based upon pollinator energetics: a flower not worth exploiting to some pollinators under some conditions may become profitable under others (e.g., Heinrich, 1975; Wolf et al., 1975, 1976).

Finally, the term "pollination unit" can be made more explicit by relating it to the breeding system of the plant (cf. Bawa, 1974; Cruden, 1977) and genetic structure of the plant population (e.g., Price & Waser, 1978). The "optimum pollination unit" might be defined as the minimum spatial separation of flowers over which movement of a given amount of pollen will produce maximum seed set (including seed viability, cf. Levin, this symposium). The "minimum pollination unit" would be the minimum separation of flowers (in terms of being on the same inflorescence, plant, or clone as well as physical distance) required for pollination to occur at all (see Stiles, 1978b). Only for obligately self-fertilizing flowers would the two terms be synonymous (the unit would be one flower in either case).

ATTRACTION

In ornithophilous flowers attraction is primarily, perhaps exclusively by color, though odor cannot be ruled out entirely in some cases (Stiles, 1976). The chief requisite for attraction is thus conspicuousness to birds, which will reflect the properties of avian vision and habitat features. Birds have their greatest spectral sensitivity and finest hue discrimination towards the long wavelength end of the visual spectrum (reviews in Sillman, 1974; Stiles, 1976), although the complex interplay of cone pigments and colored oil droplets makes the situation a great deal more complex than in mammals (e.g., Bowmaker, 1977). Moreover, hummingbirds at least may be able to perceive ultraviolet "colors" (Goldsmith, 1980); the role of this ability in foraging remains to be studied. The prevalence of ultraviolet patterns and nectar guides in relatively nectar-poor entomophilous flowers may make it possible for hummingbirds to avoid these flowers on sight. Certainly the vast majority of bird-pollinated flowers feature long wavelength colors in the attraction unit. The occurrence of other colors, or of contrasting colors, may add to conspicuousness against particular backgrounds (see Stiles, 1976). Another

factor may be the colors of the birds themselves: various authors have noted correspondences between the display colors of certain (mostly Old World) nectarivorous birds and some of their preferred flowers (Faegri & van der Pijl, 1966). Most often the colorful birds are males, who may show a hormone-mediated higher responsiveness to these colors (Ducker, 1970; Morton, 1979).

The manner in which the colors are displayed is related to a number of factors. The flower may carry the attractive colors if it is long-lived and/or in an open habitat. In many ornithophilous species immature flowers or bracts are also colorful, adding to the size and longevity of the visual signal. In other species, the need for a conspicuous, long-lived signal has been solved by the evolution of a large, colorful inflorescence (e.g., *Heliconia*, *Costus*, many bromeliads). The flowers in such cases are often ephemeral and inconspicuous except insofar as they contrast with the inflorescence, probably adaptations to help protect them from destructive nectar thieves (cf. Stiles, 1975, 1976). A variation on this theme is the incorporation of red or red-spotted leaves into the attraction unit (Jones & Rich, 1972; Stiles, 1978b).

REWARDS

Nectar is the only floral reward regularly offered to birds. Only one questionable case of regular pollen-eating has been reported for hummingbirds (Carpenter, 1976a), although it is common in parrots of the subfamily Loriinae (Churchill & Christensen, 1970; Forshaw, 1973). However, the flowers involved are often eaten by the parrots, whose role as pollinators—and hence participants in coevolutionary relationships with plants—remains to be studied in detail (cf. Paton & Ford, 1977; Ford et al., 1979).

Compared with insect-pollinated flowers, bird-pollinated flowers usually show higher nectar volumes, slightly to markedly lower concentrations, and considerably higher sugar production overall (Baker, 1975; Heinrich, 1975; Stiles, 1975, 1978b; Opler, 1981; Cruden et al., 1981). This reflects the high energy requirements of the birds, and both laboratory and field studies suggest that energetic criteria are the most important determinants of flower choice in nectarivorous birds (Hainsworth & Wolf, 1976; Stiles, 1976). The three dominant sugars in nectar, sucrose, glucose, and fructose are energetically equivalent, but sucrose usually predominates in nectars of hummingbird flowers (Stiles, 1976; Baker & Baker, 1981). Old World bird-flowers generally have nectars low in sucrose; their passerine pollinators may have difficulty digesting this sugar since experiments with European Starlings (a member of a family containing a number of facultative nectarivores) demonstrate that they cannot maintain weight on a high-sucrose diet (Schuler, 1977). Hummingbirds usually prefer sucrose-rich nectars in the field and under appropriate laboratory conditions (Stiles, 1976), but will use Old World bird-flowers freely in gardens, doubtless because of their high nectar volumes (Stiles, 1973, 1976).

Other components of nectar include amino acids, lipids, and polysaccharides (Baker & Baker, 1975). Probably none of these is nutritionally essential to nectar-feeding birds, which have access to such substances in insects and fruit, unlike most insect pollinators (cf. Baker & Baker, 1975; Gilbert, 1975; Ford & Paton,

TABLE 1. Rates of nectar extraction and feeding preferences among hummingbirds visiting two species of *Heliconia* in a Costa Rican second-growth area.^a

Hummingbird Species	<i>Heliconia</i> Species			
	<i>Heliconia latispatha</i>		<i>Heliconia imbricata</i>	
	Slope of Ex- traction Line ^b	# Visits ^c	Slope of Ex- traction Line	# Visits
<i>Amazilia tzactl</i>	0.097	182	0.176	119
<i>Thalurania furcata</i>	0.125	70	0.119	201
<i>Chalybura urochrysia</i>	0.252	36	0.112	149
<i>Phaethornis superciliosus</i>	0.322	13	0.252	88

^a Observations made June–Aug. 1971, 1972, 1974 in an area ca. 3 ha in size, of old second growth; *H. imbricata* was about 1½ times as abundant (in terms of numbers of flowers) as *H. latispatha* overall.

^b Slope of the line of time spent probing flowers (*y* axis) vs. nectar extracted (*x* axis): the lower the slope, the more nectar can be extracted in a given time. Based on 35 or more observations except *C. urochrysia*-*H. latispatha* (*N* = 21) and *P. superciliosus*-*H. latispatha* (*N* = 13).

^c Number of times a bird of a given species was seen visiting flowers of a given plant species during census walks through the study area. Each species shows a highly significant preference (*P* < 0.01 by chi-square test) for the flower at which it can most quickly extract nectar.

1976a). At low concentrations amino acids are not detected by hummingbirds; at high concentrations, they are rejected (Hainsworth & Wolf, 1976). This should place a selective premium on reducing amino acid concentrations in nectar, and Baker & Baker (1975) have indeed found that tropical bird-flowers have nectars with very low amino acid content. The more recently evolved North American hummingbird flowers have higher amino acid concentrations in their nectars—but still markedly lower than those of the presumably ancestral bee-pollinated species (Grant & Grant, 1968; Baker & Baker, 1975).

FILTERING MECHANISMS

I will discuss two sorts of mechanisms here: those tending to restrict visitation by nonpollinating animals, especially destructive ones; and those that enhance specificity of flower choice among potential bird pollinators.

Insect visitation may be reduced in bird flowers by a variety of mechanisms: red color (in addition to its conspicuousness to birds, this color is relatively inconspicuous to some bees, although probably not to many butterflies (Raven, 1972), dilute nectar (Baker, 1975; Bolten & Feinsinger, 1977), appropriate timing of nectar production (Stiles, 1975), and perhaps nectar composition. If taste conditioning occurs in insects as well as hummingbirds, the production of high-sucrose nectar may in itself favor hummingbird visitation (cf. Stiles, 1976). The hard floral parts and large nectar-sexual sphere distance mentioned in Table 1 more likely evolved as protection against destructive nectar thieves than against the “hard beaks” of pollinating birds. Opler (1981) demonstrated a direct correlation between nectar flow and flower weight among a large number of tropical plant species: the increase in weight coming largely from harder and thicker protective tissues in the perianth, as well as a longer corolla tube. In humming-

birds and presumably sunbirds the birds do not thrust the bill any further into the flower than necessary to enable the extensible tongue to reach the nectar; the tongue grooves fill with nectar most effectively in a confined space if the tongue is extended beyond the bill tip (Hainsworth, 1973; Schlamowitz et al., 1976).

Restricting visitation to a few of the potential pollinators can promote efficiency of pollination by reducing the frequency of mixed pollen loads. Specificity of flower choice, or "flower constancy," is important at the level of the individual pollinator; degree of specificity probably reflects the relative energetic profitabilities of the flowers available to each forager (Heinrich, 1976). Amount of nectar available, efficiency of nectar extraction, and cost of transport between flowers are probably the most important factors determining profitability at this level (Wolf et al., 1975). Different lengths and/or curvatures of corolla tubes can affect the extraction efficiencies of different hummingbird species in relation to differences (often subtle) in bill morphology; this in turn may strongly influence flower choice by the birds (for an example involving *Heliconia*, see Table 1: in each case the bird strongly prefers the species of *Heliconia* from which it can most efficiently extract nectar). Tubular flowers have the further effect of forcing the bird to orient its bill in a particular way when probing the flower, especially when bill and corolla are curved; this in turn facilitates placing pollen on a specific part of the bird, which can reduce mixing of pollen loads even on a relatively nonspecific pollinator (clearly an advantage for a rare plant species). This can open the way for a variety of highly specific morphological coadaptations (cf. Stiles, 1975; Brown & Kodric-Brown, 1979).

Bird flowers mostly fall into two broad morphological groups: tube and brush. Tubular flowers are in many respects the most highly evolved and the most likely to enter into specific coevolutionary relationships. Brush flowers generally house the nectar in a cup or short tube, out from which a "brush" of stamens extends. Visitors seeking nectar (or pollen) are liberally dusted with pollen, which is brought more or less haphazardly in contact with the stigmas. Many bee- and bat-pollinated flowers are of similar construction, and it may be that brush flowers simply represent a generalized adaptation to pollinators large in relation to flower size. As such they would be very ineffective filters—any visitor in a given size range could pollinate the flower. Brush flowers may, in effect, be specialized for pollination by a wide spectrum of taxonomically diverse visitors. For instance, the red stamens of *Calliandra* spp. (Mimosaceae) may represent an adaptation for drawing birds into an essentially chiropterophilous syndrome. Many regular pollinators of brush flowers are quite unspecialized in their flower visitation, such that pollination occurs more or less haphazardly as the animal blunders about in or on the flower. Such "mess and soil" pollination (Faegri & van der Pijl, 1966) may be carried out by bats, nonflying mammals (Carpenter, 1976a; Sussman & Raven, 1978), and birds such as lorries. Nectar in brush flowers is available to any visitor that does not mind getting dusted with pollen; the potential for exclusive coevolutionary relationships is low.

Pollinator specificity can be enhanced if interspecific competition occurs between potential pollinators. Aggressive behavior and/or territoriality of dominant individuals or species can result in partial or complete exclusion of subordinate individuals and/or species from flowers that they might otherwise visit (Lyon,

1976; Wolf et al., 1976). The wide range in nectar production among sympatric hummingbird flowers may function in part as a resource gradient along which different hummingbirds might specialize according to their dominance status and energy needs (Feinsinger & Colwell, 1978; Stiles, 1978b).

POLLINATION UNITS

The production of relatively large amounts of nectar and protective tissue makes bird pollination quite expensive on a per-flower basis. Thus bird pollination will probably evolve only where the advantages, in terms of enhanced pollination, outweigh these expenses (see review in Stiles, 1978b). The pollination strategy of an ornithophilous plant amounts to making enough nectar available to attract avian visitors, while adjusting their movements between flowers to the size of the optimal (or minimal) pollination unit. This entails adjusting nectar availability in terms of the proportion of the pollinator's energy requirements that can be satisfied by a single flower, shoot, or clone, and thus determining the degree of interplant movement (Heinrich & Raven, 1972).

Bearing in mind that they but represent the ends of a continuum, we can distinguish two extreme foraging tactics of nectarivorous birds: route foraging or traplining, and territoriality (Feinsinger, 1976; Stiles & Wolf, 1979). The former is ideal for promoting cross-pollination, but if the plants are widely scattered many flowers may be missed. Territoriality restricts pollen flow to and from the defended area, but its effect on cross-pollination depends on the effectiveness of the defense, and on whether the territory itself contains one or many plants (Linhart, 1973; Ray et al., 1981). Within the territory, systematic foraging of the resident may maximize the proportion of flowers visited (Gill & Wolf, 1975; Stiles, 1978b). Whether territorial or traplining pollinators are favored will depend ultimately upon the plant's spatial dispersion and breeding system, and various parameters of morphology and phenology can be varied to favor one or the other type of pollinator, as has occurred in *Heliconia* (Stiles, 1975, 1979).

AVIAN ADAPTATIONS FOR FLOWER-FEEDING

I now wish to treat the various possible avian specializations for visiting and (at least in some cases) pollinating flowers. Although virtually all of these adaptations have been discussed previously, I know of no recent attempt to bring them together to present, in effect, a coherent "syndrome of anthophily" of the birds. This would seem to be a necessary first step in assessing the degree of specialization for flower visiting of any given species or group; this in turn could provide an indication of the overall evolutionary development of bird-flower coadaptations in any given region. The features listed in my "syndrome of anthophily" (Table 2) stress relative degree of specialization; a bird may be considered more or less specialized for flower visiting according to the extent to which it shows any particular array of features to a greater or lesser extent than do its nonanthophilous closest relatives or putative ancestors (where known). This procedure may somewhat deemphasize absolute degree of specialization in those cases where a group is in some way preadapted for flower visiting. For instance, small size may be viewed as a specialization for flower visitation (see below). The

TABLE 2. Specialization for flower-feeding in birds: the "syndrome of anthophily."

Characteristics of Birds	Characteristics of Flowers
1. Small body size; usually less than 20 grams	1. Most flowers small, nectar content usually 200 μ l or less
2. Bill usually slender, often long and/or curved, matching flower corollas; occasionally hooked, awl-pointed, etc.; nasal operculum well developed	2. Nectar deep-seated, often at end of long and/or curved tube; hard flower parts (to be surpassed by nectar-robbers)
3. Tongue tip grooved, fringed, and/or capable of rolling into tube to take up nectar by capillarity, tongue extensible beyond bill tip; papillate tip for pollen feeders	3. Nectar relatively dilute, low viscosity, often in deep-seated chamber with narrow entrance
4. Gut with extensible crop for storage and rapid absorption of nectar, esophagus and intestinal openings close together, leaving stomach as a diverticulum into which insects pass, but little nectar (not necessary for pollen feeders)	4. Nectar with low amino acid content, main protein source insects.
5. Agility to reach flowers, especially hovering flight, sometimes large or strong feet to cling to inflorescence	5. Flower hangs free or faces outward or down to discourage insects
6. Aggressive behavior and often feeding territoriality well developed whenever flowers sufficiently abundant	6. Flowers stationary, visible, highly defensible resource
7. Excellent spatial memory; can recall location of flowers last visited in a dense array, or of flower clumps over wide areas and for long time periods	7. Flowers stationary, seasonal, patchy in distribution
8. Wide-ranging; seasonal movements on basis of flower abundance shifts	8. Spatial and temporal variations in blooming
9. Breeding and/or molt closely tied to flower abundance; nectar a necessary source of energy to meet expenses	9. Regularly recurring peak(s) of flowering each year, permitting birds to schedule their peak energy demands accordingly

Tennessee Warbler (*Vermivora peregrina*), a frequent flower visitor, is sufficiently small to be considered moderately specialized in this respect (8–9 g). However, its closest relatives in the genus *Vermivora* weigh scarcely more (8–11 g) but, like most of the family Parulidae, rarely or never visit flowers. Hence, the degree of actual specialization in size of *V. peregrina* is at best slight.

Many of the features listed in Table 2 are straightforward and well known, others may require some explanation. Small size (nearly always under 20 g) is common to virtually all specialized avian nectarivores, but within this size range several selective factors can operate: larger size favors social dominance, but reduces the number of flower species that can be profitably exploited (cf. Lyon, 1976; Wolf et al., 1975); small size may favor utilization of torpor as an energy-saving device (Hainsworth et al., 1977; Brown et al., 1978). With regard to locomotion, hovering ability is probably the ultimate specialization in that it permits exploitation of free-hanging blossoms, which give the greatest protection against insect visitation (Faegri & van der Pijl, 1966). However, for nonhovering species, the ability to cling acrobatically to flowers and inflorescences might be manifested in terms of larger feet than nonnectarivorous relatives, especially if these are

typical foliage-gleaning types. In the hummingbirds, where most species hover to feed, the ability to perch while feeding might reduce the costs of nectar extraction, especially for larger species (Wolf et al., 1972, 1975). I know of no small (<4 g) hummingbird that regularly clings to flowers to feed, but many medium-to-large species do, especially in the highlands (Wolf et al., 1976; Stiles, unpublished data). It is probably no coincidence that *Eutoxeres* spp., by far the largest hermit hummingbirds (10–13 vs. 2½–7 g), are also the only ones to regularly cling to flowers to feed and have extraordinarily powerful feet.

The nasal operculum is a fleshy flap that largely covers the nostrils in nectar-feeders; it presumably prevents nectar and pollen from clogging the nasal passages. It may serve as an index of nectarivory in some cases, such as the Coerebidae: it is highly developed in *Diglossa* and *Coereba*, which are highly nectarivorous; and but slightly developed in most other members of the family, who are but occasional, facultative nectarivores (see below).

The bills of nectarivorous birds are important not only as indicators of flower-feeding *per se*; they also reflect the manner of nectar extraction (e.g., whether by piercing, mashing or probing), as well as the diversity and specificity of bird-flower coadaptations that may occur within a region or community—and indirectly, the relative age of the bird-flower association there (e.g., comparing North American vs. neotropical bird-flower communities: cf. Snow & Snow, 1972, 1980; Brown & Kodric-Brown, 1979). However, low bill-flower diversity may exist in a relatively old bird-flower association if specificity *per se* is not highly advantageous (see below and Paton & Ford, 1977).

Specializations of the gut for nectar-feeding are relatively clear-cut, although in such groups as the Dicaeidae, adaptations for nectarivory may overlap with, or be subordinate to, those for frugivory (Docters van Leeuwen, 1954). Brush-tipped tongues occur in several groups that feed on fruit juices as well as (or instead of) nectar (e.g., the Zosteropidae and Coerebidae). No particular gross morphological specialization appears in the gut of the Loriinae: the nectar taken is mainly absorbed in the crop (present in parrots generally), and pollen digestion appears within the capacities of the usual psittacine gut apparatus (Churchill & Christensen, 1970; Forshaw, 1973), although enzymatic specializations may exist. I know of no features of plumage or integument that could be unequivocally interpreted as specializations for flower visitation: feathers in general have an ideal texture for pollen transport (Faegri & van der Pijl, 1966). The bright colors of some (but by no means all) nectar-feeding birds may have evolved in part as aggressive signals in relation to feeding territories, but there is little to suggest that they have evolved to match the flowers they feed on; if anything, the reverse may be true in some cases (e.g., Morton, 1979).

It is precisely in evaluating behavioral specialization for flower feeding that one encounters the greatest difficulties: not only is there much variation between and among different groups, but critical data are scarce or lacking in many cases. The ecological characteristics of flowers as a food source—stationary, conspicuous, renewable, more or less repeatable from one year to the next—allow some deductions about possible behavioral specializations. The aggressiveness and frequent feeding territoriality of nectar-feeding birds follow from these features (Gill, 1971; Stiles, 1973; Carpenter, 1978; Wolf & Wolf, 1976, etc.). By contrast, rela-

tively few data are available on spatial memory of nectarivores, especially in relation to other birds (Gass, 1978). Flower-feeding does not seem to be correlated with promiscuous or polygynous mating systems, contrary to my earlier prediction based upon hummingbirds (Stiles, 1973). Rather, the kinds of social behavior (flocking vs. solitary, monogamous vs. promiscuous, etc.) may affect foraging patterns and thus selection for bird pollination in plants of different phenologies and growth habits (see below and Stiles, 1978b).

THE MAJOR GROUPS OF FLOWER-VISITING BIRDS

Table 3 represents an attempt to compare semiquantitatively the principal groups of flower-feeding birds in terms of their degree of specialization for (and dependence upon) a nectar (or pollen) diet. I use a scale running from 0 = no particular specialization, to 3 = relatively highly specialized, as compared to non-nectarivorous near relatives or putative ancestors (known or hypothetical). The results of this analysis are expressed in terms of an approximate mean degree of specialization for the group in question, and a corresponding figure for the most specialized species in each group. Obviously these figures are an oversimplification: the various criteria used (Table 2) are not necessarily equivalent (at least in any quantitative sense), and specialization in different ways can lead to a similar overall mean. Moreover, the species within each group can exhibit a wide range of specialization according to any given criterion. For many species (indeed, for most species of many groups) published information is inadequate for an accurate assessment of specialization, and the value(s) presented represent simply my best guess. If anything, I have probably been too conservative in judging specialization according to certain criteria (e.g., annual cycles); more detailed study of the group in question might indicate rather a higher degree of specialization than I have assigned (at least for some species). Nevertheless, provided due caution is exercised, I think that these results are useful in comparing the relative specializations of the different groups of nectar-feeding birds, at least to a first approximation. This in turn will facilitate comparison of the total spectra of nectarivorous birds on each continent or major biogeographical region, and the kind and degree of bird-flower coevolution likely within each.

Several conclusions emerge from this analysis. First, by virtually every criterion the hummingbirds are the most specialized avian nectarivores. The most specialized hummingbirds are tightly tied to flowers in nearly every aspect of their biology and are often highly coevolved with a small number of flower species. Such species as *Ensifera ensifera* are totally dependent on specific flower species (in this case, *Passiflora mixta*: Snow & Snow, 1980) for critical energy supplies, just as the flowers require the bird for successful pollination. The extreme degree of bill-corolla exclusiveness in such cases is simply an indication of specialization in numerous other aspects of the biology of bird and plant. Similar but less extreme degrees of specialization are frequent in the group (e.g., Stiles, 1973; Stiles & Wolf, 1979; Wolf & Stiles 1970). Some hummingbird species, although highly dependent upon flowers, obtain nectar almost exclusively by piercing corollas (e.g., *Heliostyris barroti*); thus their potential for forming coevolutionary relationships with particular flower species is low. It is also worth

TABLE 3. Degrees of specialization for flower-feeding of the major groups of flower-visiting birds of the world.^a

Group (or Representative Specialized Species) ^c	Relative Degree of Specialization (Criteria of Table 2) ^b										References
	Body Size	Bill and Related Structures	Tongue	Digestive Tract	Loco-motion	Aggressive, Territorial and/or Foraging Behavior	Annual Cycle	Formation of Specific Coevolutionary Relationships	Mean Overall Specialization	Approx. Maximum Specialization	
Loriinae (Lories)	1	0-1	3	0-1	0	0	1	0-1	0.81	1.00	8,11,30,31
Trochilidae (Hummingbirds)	3	3	3	3	3	2-3	3	1-3	2.62	3.00	7,14,23-28,36
Meliphagidae (Honeyeaters)	1-2	1-2	2-3	2-3	0-1?	1-3	1-3?	1-2	1.75	2.37	1,7,15,18,27,30,31,33
<i>Promerops cafer</i> (Cape Sugarbird)	1	2	3	3	0	2	3	3	2.12	—	5,20
Nectariniidae (Sunbirds)	2	2-3	3	3	0-1	2-3	3	2-3	2.37	2.62	1,13,19,21,27,29
Dicaeidae (Flowerpeckers)	1-2	1	2-3	2	0	0-1	1	2-3	1.31	1.62	1,10,27,33
Zosteropidae (White-eyes)	1-2	1	1-2	0-1	0	0-1	0-2	1	0.87	1.25	1,12,27,31
<i>Zosterops olivaceae</i> (Reunion White-eye)	2	2	2-3	1	0	3	2	2-3	1.87	—	12
Drepanidae (Hawaiian Honeycreepers)	1-2	2-3	2-3	2	0	2+	2+	1-3	1.81	2.13	1,6,7,27,32
Coerebidae (Honeycreepers)	1-2	1-2	2-3	2	0-1	0-2	1-3	0-1	1.43	1.87	2,4,17,22,24,26
<i>Diglossa baritula</i> (Slaty Flowerpiercer)	2	3	3	2	1	2	3	0	2.00	—	22,24,26,34
<i>Icterus</i> (American orioles)	0-1	1	0-2?	0	0	1-2	0-1	1-2	0.62	1.00	3,9,16,26
<i>Icterus spurius</i> (Orchard orioles)	1	1	2?	0	0	2	1	2+	1.12	—	3,9,16,26
<i>Vermivora peregrina</i> (Tennessee warbler)	0-1	0	0	0	0	2	0-1	0-1	0.62	—	26,35

^a Not included are several small groups for which insufficient data exist to judge specializations: Irenidae, Calleidae (*Philesturnus*), Philepittidae (*Neodrepanis*), etc.; also omitted are numerous families some of whose members take nectar with some regularity, but show little or no specialization for flower-visiting *per se*: Sturnidae, Drongidae, Pycnonotidae, Thraupidae, Parulidae, Fringillidae, etc.

^b 0 = no particular specialization for flower-feeding (relative to related groups or putative ancestors); 1 = slight specialization; 2 = moderate specialization; 3 = high degree of specialization (dependent upon flowers).

^c Representative specialized species are often much more specialized than the group as a whole.

^d References: 1. Austin, 1961; 2. Biaggi, 1955; 3. Beecher, 1950; 4. Beecher, 1951a; 5. Broekhuysen, 1959; 6. Carpenter, 1976b; 7. Carpenter, 1978; 8. Churchill & Christenson, 1970; 9. Cruden & Toledo, 1977; 10. Docters van Leeuwen, 1954; 11. Forshaw, 1973; 12. Gill, 1971; 13. Gill & Wolf, 1975; 14. Hainsworth, 1973; 15. Keast, 1968; 16. Morton, 1980; 17. Moynihan, 1963; 18. Officer, 1964; 19. Schlamowitz et al., 1976; 20. Skead, 1963; 21. Skead, 1967; 22. Skutch, 1962; 23. Skutch, 1975; 24. Snow & Snow, 1971; 25. Stiles, 1973; 26. Stiles, pers. obs.; 27. Thomson, 1964; 28. Wolf, 1970; 29. Wolf & Wolf, 1976; 30. Paton & Ford, 1977; 31. Ford et al., 1979; 32. Raikow, 1976; 33. Terborgh & Diamond, 1970; 34. Lyon & Chadek, 1971; 35. Tramer & Kemp, 1979; 36. Snow & Snow, 1980.

emphasizing that bill-corolla morphologies are useful, but hardly infallible guides to bird-flower coevolution. Extreme bill types need not always indicate highly exclusive relationships: consider those species of *Heliconia* (the "pogonantha group" of Stiles, 1979) that show a rather high degree of morphological coadaptation with the Sicklebills (*Eutoxeres* spp.), yet are often pollinated mostly by—and are often critical food resources for—hermits of the genus *Phaethornis* (Stiles & Wolf, 1979). Conversely, some hummingbirds of relatively generalized bill type (straight, ca. 20 mm long) can become quite highly coevolved with particular flowers by virtue of their ecological situation (e.g., Stiles, 1973; Wolf et al., 1976). Thus a realistic evaluation of bird-flower coevolution often requires detailed ecological data, and these are available for relatively few groups.

In most respects the sunbirds (Nectariniidae) qualify as the next most highly specialized group of avian nectarivores. The spate of recent studies on sunbirds by Wolf, Gill, and their coworkers in Africa have demonstrated that these birds are highly adapted for flower visitation in many aspects of their foraging and aggressive behavior (e.g., Gill & Wolf, 1975, 1977, 1978; Wolf et al., 1975). Information on breeding and annual cycles is relatively sparse, but tends to indicate that at least some species approach the degree of specialization in many hummingbirds (cf. Skead, 1967; Wolf & Wolf, 1976, and included references). However, there appear to be few highly exclusive coevolutionary relationships between specific sunbird species and flowers. Most sunbird-flowers can be exploited and pollinated by several sunbird species (Skead, 1967; Gill & Wolf, 1978). Possible exceptions include certain high montane sunbird-*Lobelia* associations (cf. Chapin, 1954) and the *Arachnothera-Musa superba* association in India. In the latter instance, the very long-billed, dull-colored *Arachnothera* sunbirds evidently pollinate widely dispersed riparian clumps of *Musa* in almost exactly the same manner as hermit hummingbirds pollinate certain species of *Heliconia* (P. Davidar, pers. comm.; cf. Stiles, 1975, and below).

Slightly less specialized overall are the honeyeaters (Meliphagidae), but within this group there is a wide range of variation, from species as specialized as most sunbirds (e.g., *Promerops* spp., *Philydonyrus novaehollandae*: Broekhuysen, 1959; Paton & Ford, 1977) to a number of species that rarely or never visit flowers at all (Officer, 1964). It is thought that Australia was originally colonized by a slightly to moderately specialized nectarivore stock, which subsequently radiated to fill many nonnectarivore niches in a depauperate avifauna (Austin, 1961; Keast, 1976). A great range of adaptations also occur in the monophyletic Drepanididae of Hawaii, from highly specialized nectarivores to species adapted to a variety of totally different niches. In this case the ancestral form was probably a cardueline finch, and the highly specialized nectarivores represent an end point, rather than a starting point of diversification. Unfortunately, the most specialized Hawaiian nectarivores (*Drepanis* spp.) are now extinct (cf. Amadon, 1950; Baldwin, 1952; Carpenter, 1976b, 1978; Raikow, 1976). The case of the Dicaeidae is exceptional, as many species have evidently formed a tight coevolutionary relationship with certain mistletoes, involving not only pollination but also seed dispersal; adaptations to the latter appear to have taken precedence over those to the former (Docters van Leeuwen, 1954). In no other case known to me are the pollinators of a plant also its regular dispersers.

The coerebids or honeycreepers are a polyphyletic group, some members of which are probably descended from emberizine finches (the genus *Diglossa*, the flower-piercers), some from the tanagers (*Dacnis*, *Chlorophanes*, and related genera), perhaps some from the wood-warblers; the Bananaquit (*Coereba*) is of uncertain affinities (Beecher, 1951b; Skutch, 1962; R. W. Storer, pers. comm.). The most highly nectarivorous members of the group (*Diglossa*, *Coereba*) are quite highly specialized and dependent upon floral nectar as an energy source, but they are essentially parasites on hummingbird-flower systems, usually (*Coereba*) or virtually always (*Diglossa*) piercing the corollas of the flowers they visit (e.g., Colwell, 1973; Colwell et al., 1974). *Coereba* is a legitimate pollinator of a few plant species (Feinsinger et al., 1979). The remainder of the Coerebidae are at best facultative nectarivores whose staple foods are insects and fruit (Skutch, 1962; Snow & Snow, 1971; pers. obs.).

Because of their flower-destroying tendencies, the lories can perhaps best be regarded (at least in part) as parasites on coevolutionary relationships between flowers and honeyeaters or sunbirds. The parrots as a whole (at least in the New World) are endosperm specialists, which have evolved as specialized parasites on (mostly) animal-mediated seed dispersal systems; the lories appear to have shifted this general way of life over to flower visitation. Nevertheless, lories may accomplish some "mess and soil" pollination, especially of *Eucalyptus* (Paton & Ford, 1977; Ford et al., 1979).

A number of avian families show a relatively low (perhaps incipient?) degree of specialization for flower-feeding, at least in some species. The white-eyes (*Zosteropidae*) and American orioles (*Icterus*, Icteridae) are typical: most species are generalists, taking much fruit and insects as well as varying amounts of nectar. However, a few white-eyes are markedly more closely associated with flowers than the rest, approaching some sunbirds in degree of specialization (Gill, 1971). Some species of *Icterus* are the major pollinators of certain plant species (e.g., Cruden & Toledo, 1977). Other families contain a sprinkling of species that are behaviorally, but not morphologically, slightly to moderately specialized for flower visitation (e.g., *Vermivora peregrina* of the Parulidae, see above; also certain members of the Sturnidae (Starlings), Dicruridae (Drongos), Irenidae (Leafbirds), Pycnonotidae (Bulbuls), Thraupidae (Tanagers), etc.). Finally, there is a large number of families for which scattered reports of flower visitation exist, but for which there is no indication that nectar is important in their diets, or that they are in any way specialized for acquiring it. These species have little importance in bird-flower coevolutionary systems and will not be discussed further here (although collectively they may play some role in pollination of very generalized brush or "cornucopia" flowers, cf. Faegri & van der Pijl, 1966).

A GEOGRAPHICAL SURVEY OF BIRD-FLOWER COEVOLUTION

At the level of zoogeographical regions, the Neotropical undoubtedly contains the most highly specialized, as well as the largest (over 300 species in the Trochilidae alone) assemblage of flower-feeding birds (Table 4). Each of the Palearctic realms contains perhaps 100–150 species of passerine nectarivores, many of which are at most only slightly specialized. The Ethiopian region contains the

TABLE 4. Nectar-feeding bird assemblages of different zoogeographical regions.

Group	Approximate Number of Species in Region					
	Neo-tropical	Ne-arctic	Palae-arctic	Ethio-pian	Ori-ental	Austral-Asian
Loriinae (Lories)	0	0	0	0	2	ca. 50
Trochilidae (Hummingbirds)	315	ca. 10	0	0	0	0
Meliphagidae (Honeyeaters)	0	0	0	2	0	160 ^a
Philepittidae (False-sunbirds)	0	0	0	2	0	0
Nectariniidae (Sunbirds)	0	0	ca. 5	ca. 60	ca. 35	ca. 13
Chloropseidae (Leafbirds et al.)	0	0	0	0	ca. 10 ^a	0
Dicaeidae (Flowerpeckers)	0	0	2	0	ca. 30 ^a	ca. 25 ^a
Zosteropidae (White-eyes)	0	0	2	ca. 15 ^a	ca. 60 ^a	ca. 10 ^a
Coerebidae (Honeycreepers)	ca. 15 ^b	0	0	0	0	0
Icteridae (American orioles and blackbirds)	ca. 20 ^b	3+	0	0	0	0
Others ^c	100+	ca. 20	0?	75+	50+	50+

^a Many of these species are not at all closely associated with flowers and should be considered facultative nectarivores at best, but detailed data not available.

^b Includes only those species known or suspected to be highly nectarivorous (at least at some phase of their annual cycle).

^c Includes mostly casual or facultative, and/or unspecialized nectarivores; numbers are mostly rough guesses based upon a variety of casual observations and statements in the literature (e.g., in faunal lists, etc.).

bulk of the rather highly specialized sunbirds and perhaps the most specialized meliphagids (*Promerops*), as well as many species in a variety of families (e.g., Sturnidae, Pycnonotidae, Zosteropidae, etc.) that are considerably less specialized. Several families in the Oriental region contain nectarivorous species, but except for the sunbirds, most would not appear to be highly specialized for flower-visiting. There are virtually no detailed, critical studies of nectar-feeding birds for this entire realm, most of the published information being highly anecdotal in nature. However, it appears to me that this is the tropical region with the smallest assemblage of obligate, highly specialized nectarivores; conversely, there is apparently a relatively large and diverse group of facultative or occasional flower visitors. The collective impacts of these two groups, and the importance of bird pollination in the region as a whole, remain to be evaluated critically. The Australasian region contains virtually the entire large family Meliphagidae, but at most half of these are strongly associated with flowers (Officer, 1964; see also Ford et al., 1979). Also occurring here are the primarily pollen-feeding Loriinae, and a few species of sunbirds and dicaeids. Particularly in New Guinea, a number of species of other groups may be occasionally associated with flowers, but the dominant groups (in terms of numbers of species) in both New Guinea and Australia are the honeyeaters and lories (Terborgh & Diamond, 1970; Paton & Ford, 1977). The Nearctic realm contains a small contingent of hummingbirds obviously derived recently from the Neotropical; it also contains a number of migratory species (*Icterus*, certain Parulidae like *Vermivora peregrina*) that are seldom or never associated with flowers on their breeding areas, but which migrate during the nonbreeding season to the Neotropical realm where they may be quite nectarivorous. Finally nearly the entire Palaeartic realm has

no native flower-visiting birds or bird-pollinated flowers (this was doubtless responsible for the long controversy in the European literature regarding the existence of bird pollination). A few nectarivorous birds do occur in peripheral areas of this region (the Middle East, east Asia).

The two regions for which the most detailed information on bird-flower coadaptations exists are the Neotropical and the Australasian. Bird-flower communities have evidently evolved along radically different lines in these two areas, and it seems instructive to compare the ecological roles of bird pollination systems therein. It should be mentioned at the outset that detailed data are available for only a few communities in each region; however, the patterns within regions seem to be sufficiently consistent, and differences between regions sufficiently pronounced, that the general conclusions I draw should be valid. For the Australasian region I rely mainly on the studies by Recher (1971, 1977), Ford & Paton (1976a, 1976b), Paton & Ford (1977), Ford et al. (1979), Carpenter (1978), Collins (1980), and Hopper & Brundage (1978), with Terborgh and Diamond (1970) being the only really useful reference for New Guinea. For the Neotropical region my main sources are Skutch (1962), Snow & Snow (1971, 1972, 1980), Cruden & Toledo (1977), Toledo (1975a, 1975b), Feinsinger (1976, 1978), Wolf (1970), Wolf et al. (1976), and Stiles (1973, 1975, 1978a, 1978b, 1980, and unpublished data).

In the Australian region birds are often important pollinators of major vegetation types—although in some communities their importance has perhaps been exaggerated in the past. Many of the flowers they visit and often pollinate occur in large, rich, dense patches (e.g., large trees like *Eucalyptus*, dense clumps like *Anizognathus*). Nectar is often extremely abundant locally, so much so that the birds present cannot come near to exhausting it. In such sites (e.g., *Protea* heath) the major pollinators may actually be nonflying mammals (Carpenter, 1978; see also Sussman & Raven, 1978). Between these nectar flushes may be long periods of low nectar availability; many of the birds are nomadic and their movements are tied to blooming periods of major food plants. Breeding of the birds may be tied to nectar supplies, or—especially for the larger species—limited by insect availability. The birds are in general social: most honeyeaters and lorries move in groups or flocks, usually traveling between large, transient resource patches.

Perhaps the most striking characteristic of the bird-flower system in Australia is the lack of specificity: as Paton and Ford put it, the birds seem adapted to the flora as a whole, the plants to the Meliphagidae as a whole. Most nectar-feeding honeyeaters of an area are capable of pollinating most of the ornithophilous flowers of the area. The majority of these flowers are of the brush type, with its inherently low filtering ability; this permits mammals to play a major role as pollinators in some cases. Tubular flowers are by no means rare, but the tubes are short, often of the "gullet" type with lateral slits, such that the nectar is accessible to birds with a wide range of bill lengths (Ford et al., 1979). This lack of specificity may be related to the dry, unpredictable climate of much of Australia: at any given site the timing and intensity of flowering may vary greatly from year to year, and the birds evidently track flowering bursts only approximately.

Where flower specificity occurs in Australian plants, it appears more in those flowers with tubular corollas like *Anizognathus* spp. Hopper & Brundage (1978)

found that individuals of the common pollinator of two species of *Anizognathus* (the meliphagid *Anthochaera carunculata*) showed 97% fidelity to each species, but this reflected mainly temporal differences in peak blooming periods and different flower placement, such that different techniques were required to exploit each species. However, there was no suggestion that different honeyeater species were visiting different flower species.

This general picture seems to hold in New Guinea also: different species of flowering trees attract essentially the same spectrum of avian visitors. The birds partition the floral resources according to height, density, and location on the trees, rather than by tree species. This system would well repay further study with marked birds and controlled pollinations. The fact that the overall bird-flower system in wet, tropical New Guinea resembles more the situation in dry subtropical Australia rather than that in wet neotropical areas doubtless reflects in part differing taxonomic affinities and social systems of the birds; but more data are clearly needed before a detailed explanation should be attempted.

The situation in Africa seems to resemble that in the Australasian region in many respects: floral resources occur in large patches that are exploited by several species, at least at some times of the year. However, dominance interactions and territoriality, as well as differences in foraging efficiency, may play more of a role in structuring avian exploitation of the mostly tubular flowers (Gill & Wolf, 1978). However, more detailed studies over the entire annual cycle are definitely needed.

Neotropical bird-flower communities are structured along very different lines than those of Australasia. This region is especially interesting in that it contains several groups of flower-feeding birds that differ strikingly in several aspects of their biology. The dominant group numerically and ecologically is the hummingbirds. The coerebids represent a later addition to the hummingbird-flower systems that may affect the operation of these systems, especially in highland areas (cf. Colwell, 1973; Lyon & Chadek, 1971; Colwell et al., 1974). Finally, still more recent additions include a group of relatively unspecialized passerine nectarivores that may be important pollinators in some situations, and appear to be the closest ecological equivalents to many Old World groups (e.g., many meliphagids, White-eyes, etc.).

The hummingbirds are divided into two subfamilies: the hermits (Phaethorninae) and the typical hummingbirds or nonhermits (Trochilinae), which comprise ca. 90% of the family. Most hermits have long, curved bills and tend to forage at scattered flowers with long, curved, tubular corollas and high nectar flow. Such flowers are usually visited and pollinated exclusively by hermits which partition the different species largely according to microhabitat; the long curved corollas are difficult for most nonhermits to negotiate efficiently. Different hermit flowers often place pollen on different parts of the bird, and have temporally offset flowering seasons.

The nonhermit group is considerably more varied, but one may distinguish three major morphological types: medium-sized (3½–7 g) species with straight bills around 20 mm long; small, short-billed species (mostly under 3½ g with 10–15 mm bills); and a smaller number of species with long (>30 mm) and/or curved bills, medium to large in size (5½–12 g). Obviously not all of the nearly

300 nonhermits will fit neatly into these three types, but at least in Central America the great majority do.

The greatest number of nonhermit species usually falls in the first group in any given community. The amount of morphological divergence between sympatric species is often relatively slight, but even so may have a pronounced effect upon foraging efficiencies and flower choice (e.g., Table 1). Specificity of flower choice is further enhanced by dominance interactions and territoriality, as well as differences in microhabitat in some cases. However, hummingbirds of this type often partition floral resources as much by patch size or flower density as by flower species *per se*: often two or more species of hummingbird are alternate pollinators of a given flower species. The nonhermits of the second group tend to be excluded from many of the flowers exploited by the first group due either to their subordinate status, or their inability to forage efficiently due to their relatively short bills. These small hummingbirds often visit small, short-corolla flowers with nectar production too low to attract larger and more dominant species; they often share the role of pollinators with insects like butterflies or bees. The members of the third group of nonhermits often resemble hermits in their foraging, visiting flowers with long and/or curved corollas that often are scattered in small patches. These hummingbirds are most prominent in microhabitats or regions where the true hermits are scarce or absent: the canopy of wet lowland forest, dry forest, or at high elevations. Like the hermits, they may also be exclusive pollinators of some plant species by virtue of morphology.

Overall, there is thus a considerable degree of specificity of flower choice in hummingbird-flower communities—at least at the level of the morphological type of hummingbird, if not always at the level of species. Any given plant species usually receives a great majority of visits from one or a very few hummingbirds, representing a relatively small proportion of the total number of hummingbird species present. Therefore, compared with a honeyeater-flower community, one might expect greater species richness in hummingbird-flower communities. Certainly the ratio of flower species to bird species seems higher in the latter: for instance, at Finca La Selva, Costa Rica (Table 6) occur some 20 species of hummingbirds, and approximately 50 species of plants are pollinated mostly or exclusively by them. By contrast, some 21 species of ornithophilous plants near Adelaide, Australia were visited and pollinated by 25–28 species of birds (Paton & Ford, 1977). Overall, Ford et al. (1979) estimate that over 100 species of birds have been recorded as visiting the flowers of some 250 plant species in Australia. In Costa Rica alone, I have records of ca. 75 species of birds visiting the flowers of over 300 species of plants. About 55 of the birds can be considered regular flower visitors, and well over half of the plants are probably pollinated mostly or exclusively by birds (taxonomic uncertainties and lack of detailed information on pollination prevent me from venturing more precise estimates of plant species numbers).

One other geographical pattern deserves mention. In the New World, the vast majority of ornithophilous plants are herbs, shrubs, small trees, or epiphytes; very few are canopy trees. Only one out of nearly 50 hummingbird-pollinated plants at Finca La Selva is a canopy tree (*Erythrina cochleata*, which has a very small crown with sparse branching and few flowers). No trees are pollinated by

hummingbirds in a Costa Rican montane site (Wolf et al., 1976) or a California mountain area (Stiles, 1973). By contrast, many ornithophilous plants of the Old World are trees (e.g., Chapin 1954; Officer, 1964; Skead, 1967; Paton & Ford, 1977) which often form the dominant vegetation over sizeable regions (Ford et al., 1979). I think this relates to the social systems of the common flower-birds of these areas: passerine nectarivores (and lorries) of the Old World tend to travel in groups or flocks, whereas hummingbirds are virtually always solitary. A large concentration of flowers, as on a large tree, would quickly be parceled up into individual feeding territories by hummingbirds (e.g., Stiles & Wolf, 1970), which could drastically reduce cross-pollination. However, the nectar resources of even a large tree could be exhausted fairly quickly by a flock of larger passerine nectarivores, which would then have to move on to the next tree—thereby effecting cross-pollination.

The role of the relatively unspecialized, recently derived passerine nectarivores of the New World—e.g., *Icterus* spp., possibly even the Tennessee Warbler *Vermivora peregrina*—is of particular interest in this connection. Many of the species of plants pollinated by these birds are large trees with abundant flowers, e.g., *Erythrina poeppigiana* and *E. fusca* (Feinsinger et al., 1979; Morton, 1979; see also Cruden & Toledo, 1977). Like Old World nectarivores, these species tend to move in groups or flocks—indeed, in appearance and behavior the Tennessee Warbler on its tropical wintering grounds seems to be the exact equivalent of a White-eye! Moreover, several ornithophilous brush-flowers of the New World are pollinated by these passerine nectarivores rather than hummingbirds (e.g., *Combretum farinosum*; Alvarez del Toro, 1963). It is also worth noting that many species of nectarivorous bats also forage in flocks, that the plants that they pollinate are often trees, and that the flowers involved are often brush-flowers (Heithaus et al., 1974).

EVOLUTIONARY PATTERNS, WITH EMPHASIS ON THE NEOTROPICS

The earliest flowering plants were probably pollinated by primitive pollen-eating insects, probably beetles (Baker & Hurd, 1968; Faegri & van der Pijl, 1966). Just how and when such a pollination system incorporated nectar as an attractant, and specialized insects and finally birds as pollinators is highly speculative. The early fossil record of flowers and their pollinators is decidedly scanty, but we do know that specialized flower-visiting bees and essentially modern bats were present by the early- to mid-Tertiary (Baker & Hurd, 1968; Raven & Sussman, 1978). Flower-visiting birds *per se* do not appear in the fossil record until the Pleistocene (cf. Thomson, 1964) but undoubtedly originated considerably earlier. The taxonomic distinctness of the specialized avian nectarivores of the Neotropical, Ethiopian, and Australasian regions (Table 3) suggest that flower-feeding as a way of life originated independently in each well after their separation by continental drift. Africa and South America share no nectar-feeding groups, and were separated by a water gap sometime in the Cretaceous (cf. Baker, 1973). Therefore, the story of bird-flower coevolution begins probably sometime in the early- to mid-Tertiary. Given that the hummingbirds are the largest, most taxonomically distinct, and most specialized group of flower-birds, it seems not un-

likely that bird-flower coevolution began relatively earlier in the New World than elsewhere.

The early evolution of the hummingbirds is shrouded in mystery, and even their affinities among modern birds remain in doubt. Hummingbirds have usually been placed in the same order as the swifts because of similarities in their flight mechanism (and small feet). However, recent morphological studies (J. Cohn, R. Zusi, pers. comm.) indicate that these similarities are most likely due to convergence; certainly hummingbirds and swifts fly rather differently. Like Skutch (1975), I find it much easier to envision the evolution of hummingbirds from a passerinelike, rather than a "primitive swiftlike" (cf. Austin, 1961) progenitor. The evolution of a bill and tongue specialized for nectar-feeding from the reduced structures adapted for aerial insect-feeding as practiced by swifts, swallows, etc., seems most unlikely. Rather, the "proto-hummingbird" might have been a small, sallying and hover-gleaning insectivore not unlike some modern parulids (e.g., Morse, 1967), that would have sought its food in the foliage (and possibly flowers) at the tips of twigs. A progressive emphasis on hovering and the concomitant decline in the role of the legs could have led to reduction of the latter. Small legs and feet that are little used in foraging occur not only in swifts and other aerial insectivores, but also—and more to the point—in specialized sally-feeders (jacamars, motmots, puffbirds, etc.) that clearly did not evolve from "swiftlike" ancestors. While it is generally agreed that the earliest visits of birds to flowers were for insects (Faegri & van der Pijl, 1966), it is worth noting that bees (and presumably nectar-containing bee flowers) were present by the time the hummingbirds presumably were evolving. These birds may have been specifically associated with nectar from the first.

Pollination by hummingbirds has long been established in the neotropics as evidenced by the families (e.g., Musaceae, Bromeliaceae) and large genera (e.g., *Cavendishia*, *Costus*, *Columnea*, *Aphelandra*) that are largely or entirely hummingbird-pollinated there. Insect (bee or lepidopteran) pollination was probably the precursor of hummingbird pollination, not only because these insects were first on the scene but because intermediate stages of the process are visible today. For example, the genus *Costus* contains many bird-pollinated species (with red or yellow flowers and/or bracts, narrow corolla tube, high nectar production) and bee-pollinated species (usually green bracts, whitish flowers with yellow or purple "nectar guides," low nectar production, broad campanulate corolla tube). *Costus malortieanus* of Costa Rica resembles bee-pollinated species in color but has an intermediate corolla tube and high nectar production; it is pollinated both by hermit hummingbirds and *Eulaema* bees (Stiles, 1978a; Stiles & Wolf, 1979; H. Kennedy, pers. comm.). Another example is *Hamelia* of the Rubiaceae, a family usually associated with lepidopteran pollination. This genus contains species pollinated by birds, butterflies, or both (pers. obs.; Opler, 1981).

EVOLUTION OF THE PHAETHORNINAE AND TROCHILINAE AND THEIR FLOWERS

Plant-pollinator relationships may also help to shed some light on the evolution of the two subfamilies of hummingbirds, the hermits and nonhermits (see above).

TABLE 5. Altitudinal distributions of hermit (Phaethorninae) and "typical" (Trochilinae) hummingbirds in three New World areas.

Area and Subfamily	Numbers of Species				
	Tropical	Premontane	Lower Montane	Montane + Subalpine	Total Species ^a
A. Costa Rica ^b					
Phaethorninae	5	3	1	0	6
Trochilinae	20	24	12	5	45
B. Colombia ^c	Tropical	Subtropical	Temperate	Paramo	
Phaethorninae	20	6	0	0	19
Trochilinae	61	60	38	10	115
C. Venezuela ^d					
Phaethorninae	13	2	0	0	13
Trochilinae	59	47	24	7	84

^a Less than the total of altitudinal zones, as many species occur in more than one altitudinal zone. However, species that barely enter a zone, or do so only rarely, are *not* counted for that zone.

^b From Slud (1964) and personal observations. Altitudinal zonation based on Holdridge life zone system.

^c From de Schauensee (1960); altitudinal zonation that of Chapman, which compares with Holdridge system as follows: "Tropical" includes much of premontane; "Subtropical" includes upper premontane, and most of lower montane; "Temperate" is nearly equivalent to montane, but includes uppermost lower montane; paramo and subalpine are essentially equivalent.

^d From de Schauensee & Phelps (1978); altitudinal zonation is the same as 3.

The hermits are basically birds of the understory of wet tropical forest; they decrease in abundance and diversity towards higher elevations or drier areas (Table 5, Fig. 1), and extend northward only to the limits of lowland "rain" forest in Veracruz, Mexico (Friedmann et al., 1950). By contrast, the nonhermits reach their greatest diversity in the tropical highlands, around 1000–1500 m elevation in Costa Rica (Table 5, Fig. 1). In wet tropical lowlands, nonhermits are most numerous in the forest canopy rather than the understory, at least for most of the year (Stiles, 1978a, 1980). Nonhermits are the most numerous group in dry tropical areas, where the hermits occur only in riparian habitats—if at all. Also, only the Trochilinae reach higher northern latitudes or occur above 2000 m elevation at tropical latitudes (cf. Snow & Snow, 1980; Stiles, pers. obs. and Fig. 1).

Each of these groups appears to have evolved for a long time in conjunction with a particular set of flowers. The hermits are virtually always associated closely with large monocotyledonous herbs of the order Scitamineae, notably the genus *Heliconia* (Table 6; also see Snow & Snow, 1980). At least 34 of the 40 known Costa Rican species of *Heliconia* (Stiles, 1979, and unpublished data) are hermit-pollinated, notably by members of the genus *Phaethornis*. Isolated species in several species-groups have secondarily become adapted for pollination by nonhermits, usually in conjunction with occupying younger second-growth habitats. Neither hermits nor *Heliconia* occur above 2000 m in Central America or northern South America, and only a single nonhermit-pollinated species occurs widely in dry and/or open areas where hermits are absent (Stiles, 1975, 1979).

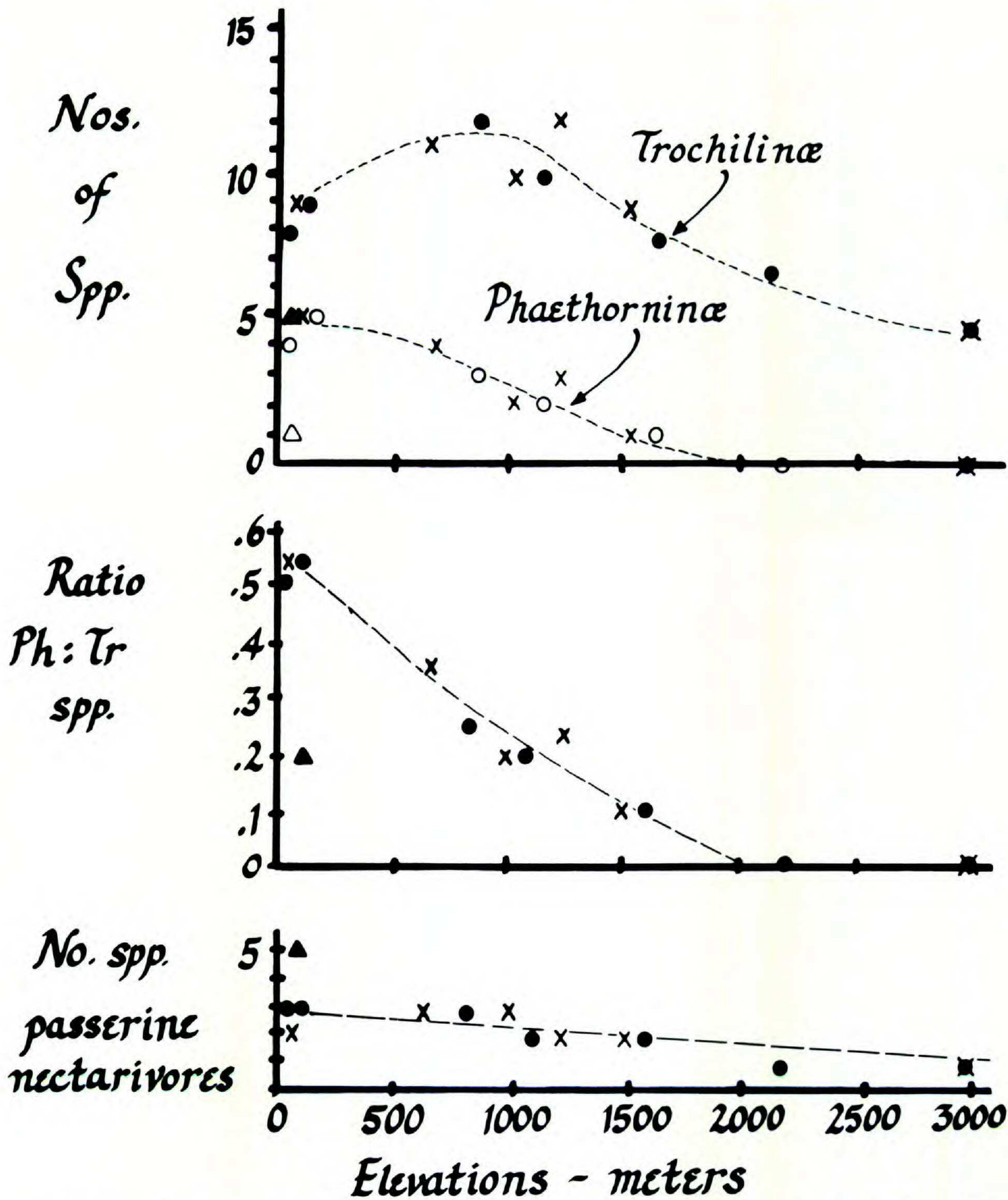


FIGURE 1. Numbers and ratios of species of hermit (Phaethorninae) and "typical" (Trochilinae) hummingbirds, and of passerine nectarivores, that are common and/or resident at 13 sites in Costa Rica at different elevations. Circles = Caribbean slope; crosses = humid Pacific slope; triangles = dry Pacific slope.

Most of the plant groups that are mostly or entirely pollinated by the non-hermits reach their greatest diversity in the tropical highlands, and most are dicots (e.g., the tribes Thibaudeae of the Ericaceae, Fuchsiae of the Onagraceae) (Table 6). The only monocot family showing close association with the Trochilinae is the Bromeliaceae; and these are mostly epiphytes of forest canopy, a habitat rarely exploited by hermits (Stiles, 1980). At Finca La Selva, Costa Rica, the

only bromeliad pollinated by hermits is a terrestrial forest species, *Aechmea magdalенаe*. With the possible exception of the Acanthaceae, all the major dicot families have a majority of nonhermit-pollinated species—although most have hermit-pollinated species as well, usually in different genera. The Rubiaceae are especially interesting in this regard: most ornithophilous species of the family have short, straight corolla tubes, clustered flowers, and relatively low nectar production, obviously adapted for nonhermit pollination. The small epiphyte *Ravnia triflora* presents an interesting contrast: the flowers open singly, and they have a very long corolla tube and relatively high nectar production. In effect, in corolla shape and nectar production, most Rubiaceae bird-pollinated flowers show affinities with the many species of the family that are pollinated by butterflies and small sphingids; a few species, like *Ravnia*, appear to resemble those more specialized species pollinated by very large and long-tongued sphingids (cf. Cruden et al., 1981). Thus it may be that the latter species are to some extent preadapted for hermit pollination in a family most of whose avian pollinators are nonhermits.

As noted above, in areas or microhabitats where the hermits are rare or absent, certain species of nonhermits and their flowers have converged on the "hermit-flower" syndrome. Examples in Costa Rica include *Eugenes fulgens* and *Campylopterus hemileucurus* at high elevations, and *Heliomaster* spp. in dry areas or in forest canopy. Where both groups occur together in tropical wet lowlands, the hermits are denizens of forest understory and light gaps; nonhermits occur chiefly in the forest canopy, at larger light gaps, and outside the forest (Slud, 1960; Stiles, 1980).

In the past, the hermits have sometimes been considered primitive (e.g., Ridgway, 1891), perhaps partly due to their lack of brilliant iridescence. I think rather that the ecological and behavioral evidence, in particular the coevolutionary relationships with different flower groups, point to a long period of separate evolution of the two groups. One could even envision the same group of "proto-hummingbirds" giving rise independently to hermits in tropical wet lowlands and to nonhermits in the highlands, during the early to mid-Tertiary. At the present time the center of diversity of the hermits is the Amazon basin, particularly the western portion. The Trochilinae attain their greatest diversity in the Andes, but this undoubtedly reflects the great burst of speciation and differentiation associated with the Pliocene-Pleistocene uplift of the Andes. The actual center of origin of the nonhermits may lie in the much older highlands of eastern Brazil.

HUMMINGBIRD-FLOWER COEVOLUTION IN NORTH AMERICA

Only a small, morphologically homogeneous group of nonhermits (currently classified in four badly oversplit genera) has succeeded in occupying North America well north of Mexico. Several factors suggest that this group has arrived relatively recently in North America and speciated there. Nearly all species are segregated geographically or by habitat during the breeding season; when two species breed in the same habitat, their breeding seasons are temporally offset (Pitelka, 1951; Stiles, 1973). With the exception of the large genus *Castilleja* (which is well represented in Mexico), North American hummingbird flowers

occur as isolated species in otherwise entomophilous genera, or as small and poorly differentiated genera (Grant & Grant, 1968).

The morphological uniformity of the hummingbirds is matched by that of their foodplants. Following their respective breeding seasons, several species of hummingbirds regularly cooccur in mountain meadows of southwestern North America, and several species of hummingbird flowers bloom simultaneously in these habitats (Grant & Grant, 1968; Stiles, 1973). The birds in such assemblages evidently do not discriminate between flower species to any marked degree, and all species of hummingbirds may pollinate any given species of flower; the flowers seem to have converged to a common color and morphology (Brown & Kodric-Brown, 1979). This overall lack of specificity brings to mind the structure of Australian bird-flower communities, rather than the more complex hummingbird-flower communities of the neotropics (see above). It is noteworthy that all North American hummingbirds are (or were, until recently; see Stiles, 1973) migratory. Their seasonal movements, coupled with the dry and variable (on a year-to-year basis) climates of western North America may add an element of unpredictability to the system that has inhibited the evolution of more specific coadaptations: flexibility may be important for both birds and flowers, as it seems to be in Australia. We definitely need more data on interyear variation in the composition and dynamics of these bird-flower assemblages to evaluate this hypothesis.

A number of species of plants in the western North American flora seem to be evolving towards hummingbird pollination, and presently possess more or less brushlike flowers (e.g., *Trichostema lanatum*, *Isomeris arborea*). Indeed, a "brush" phenotype could be interpreted as the first step towards adaptation to a larger pollinator, to be followed by a lengthened corolla tube and tighter co-evolutionary relationships. I have seen *Trichostema* visited and pollinated by both hummingbirds and large bees in California; bee pollination is almost certainly ancestral (Grant & Grant, 1968).

It is of interest that many North American species pollinated by hummingbirds, despite their relatively recent origin, appear in most respects (color, form, amount and sugar composition of nectar) to be as specialized for these pollinators as do most of the evolutionarily older tropical species (Grant & Grant, 1968; Stiles, 1976; Baker & Baker, 1981; Cruden et al., 1981). Only in the higher concentrations of amino acids in the nectars of the former is their more recent origin clearly reflected (Baker & Baker, 1975).

POLLINATION BY PERCHING BIRDS

Pollination by perching birds also appears to be of relatively recent origin in the New World, and may be primarily associated with the family Icteridae (genera *Icterus*, *Dives*, *Notiopsar*, etc.) (Toledo, 1975a; Cruden & Toledo, 1977). A range of degrees of specialization for nectar-feeding is evident in the large genus *Icterus* itself (Beecher, 1950), with the most specialized species still considerably less specialized than the major Old World nectarivores (cf. Table 3). Cruden and Toledo compare the New World passerine nectar-feeders as a whole with the facultative and relatively unspecialized Old World nectarivores of such families as the Pycnonotidae, Oriolidae, Sturnidae, etc.

TABLE 6. Taxonomic affinities of hummingbird flowers, in relation to their primary pollinators (Phaethorninae vs. Trochilinae).

	Primary Pollinator	No. Sp. of Monocots				TOTAL
		Brome- liaceae	Musaceae	Zingi- beraceae	Other	
Finca La Selva, Costa Rica	Ph.	1	6	4	1	12
pers. obs. 100 m	Tr.	7	3	1	0	11
La Montura, Costa Rica	Ph.	6	3	2	0	11
pers. obs. 1100 m	Tr.	5	1	1	1+	8+
Villa Mills, Costa Rica						
pers. obs. 3000 m	Tr.	1	0	0	2+	3+
Santa Rosa, Costa Rica ^a						
pers. obs. 150 m	Tr.	2	1	0	3	6
Arima Valley, Trinidad	Ph.	4	4	2	1	11
(Snow & Snow, 1972)	Tr.	4	0	0	0	4
Las Tuxtlas, Veracruz, Mexico	Ph.	0	1	2	0	3
(Toledo, 1973)	Tr.	2	1	0	0	3
Sta. Monica Mts. Calif.						
(Stiles, 1973)	Tr.	0	0	0	0	0
Venezuelan Andes						
pers. obs. 2000 m+	Tr.	3+	0	1+	1	5+

^a Includes a single species of hermit, the small (2.5 g), relatively generalized (bill 22 mm, nearly straight) *Phaethornis longuemareus*, which is normally restricted to gallery forest.

Another indication of the recency of passerine pollination is that the flowers involved occur as isolated species in genera adapted for pollination by hummingbirds or other agents (Toledo, 1975a, 1977; Cruden & Toledo, 1977). Passerine pollination is by no means necessarily evolved from hummingbird pollination. Such pollination systems may have evolved from bat-pollinated flowers (e.g., *Agave* and perhaps some *Marcgraviaceae*; Stiles, unpubl. data), and perhaps other systems as well. The geographical distribution of passerine nectarivores also differs from that of hummingbirds in several respects, leading one to suspect that passerine pollination is often complementary to hummingbird pollination, rather than necessarily evolved from it. In humid life zones there is only a slight decrease in the number of passerine nectarivores with altitude—and most of the latter are members of the family *Coerebidae*, which only exceptionally are *bona fide* pollinators (Fig. 1). The maximum diversity of passerine nectarivores in Central America occurs in dry tropical lowlands, where hummingbirds are relatively poorly represented (Table 6; see also Wolf, 1970). Conversely, the genus *Icterus* reaches its greatest diversity in the drier areas of Mexico and northern Central America (Beecher, 1950); passerine pollination is probably well established in the American southwest in genera like *Fouquieria* and *Agave* (Stiles, unpubl. data; Toledo, pers. comm.).

CONCLUSION

It is striking that many of the species adapted for passerine pollination appear to be as specialized for these pollinators, and in the same ways (nectar compo-

TABLE 6. Continued.

No. Spp. of Dicots										Total No. Hum- ming- bird food- plants	No. Spp. of Hummingbirds		
Acan- tha- ceae	Eri- caceae	Ges- neri- aceae	Labia- tae	Lobeli- aceae	Ona- gra- ceae	Rubi- aceae	Scroph- ulari- aceae	Other	TOTAL		Com- mon and/or Resi- dent	Rare + Irreg- ular	TOTAL
4	0	1	0	0	0	1	0	2	8	20	5	1	6
2	1	5	0	0	0	4	0	7	19	30	9	7	16
3	0	2	1	1	0	1	0	1+	9+	20+	2	2	4
3	6	7	0	1+	0	3+	0	7+	27+	35+	10	7	17
0	3	0+	2	3	3	0	1	3	15+	1	4	2	6
2	0	0	1	0	0	2	1	6	12	18	5	3 ^a	8
1	0	0	0	1	0	0	0	3	5	16	3	0	3
1	0	0	0	0	0	6	0	6	13	17	6	3	9
1	0	1	1	0	0	0	0	0	3	6	2	0	2
2	0	0	0	0	0	2	1	5	10	13	7	2	9
0	1?	0	2+	0	4	0	4	2	12	12	3	3	6
1?	4	2	4	4	4	1	2	5+	27+	31+	—	—	20+

sition, presence of perch, etc.), as are many ornithophilous species in the Old World (Cruden & Toledo, 1977; Cruden et al., 1981; Baker & Baker, 1981). These observations strongly support the hypothesis of Baker & Hurd (1968) regarding plant-pollinator coevolution in general. These authors postulate that the initial selective demand is made by the animal, as an unspecialized flower visitor; the most profound evolutionary response is by the plant, in the form of a suite of adaptations to attract the visitor consistently enough that it becomes a reliable pollinator—in short, a “syndrome” in the classical sense. The behavioral flexibility of the animal thus fits with what might be considered the evolutionary flexibility of the plant—that is, the variety of ways in which genetic variation in plant populations can be rapidly reorganized and selected, via the different mechanisms of rapid speciation in these organisms, including hybridization and polyploidy (Raven, 1980).

Further evolution of the presumptive coadapted complex could occur in various directions discussed in this paper. The pollinator could evolve towards increased specialization for, and dependence upon, floral food (a process just beginning in New World orioles, and virtually completed in the Trochilidae). Selection may favor further elaboration of the reward unit of the plant, not only in terms of filtering mechanisms to restrict reward availability to a particular subset of potential pollinators, but also through controlling the provision of energy to these so as to favor degrees of interplant movement most compatible with the optimal pollination unit (Heinrich & Raven, 1972; Stiles, 1978b). All stages of this evolutionary scenario can be found in the complex of nectarivorous birds and the flowers they visit and pollinate. Bird-flower systems are proving to be a fruitful vehicle for understanding plant-pollinator coevolution in a general sense.

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